A CARNIVOROUS SPONGE, *CHONDROCLADIA GIGANTEA* (PORIFERA: DEMOSPONGIAE: CLADORHIZIDAE), THE GIANT DEEP-SEA CLUBSPONGE FROM THE NORWEGIAN TRENCH

BETTINA KÜBLER AND DAGMAR BARTHEL

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The ultrastructure of the deep-sea sponge *Chondrocladia gigantea* from the Norwegian Sea, North Atlantic, was studied for the first time. Club-shaped, erect *C. gigantea* has a unique form of aquiferous system, not previously observed in Porifera, consisting of rows of large choanocyte chambers running through the main axis of the sponge, which explains the numerous, normally extended water-filled spheres sitting on little stalks in the upper external part of the main body. These previously enigmatic translucent spheres serve as surface extensions of the sponge to trap prey in the food-poor, deep-sea environment. In addition, they release male reproductive cells into the water. Sexual reproduction seems to play an important role in *C. gigantea*, since spermatocysts were found at different stages of maturity in two out of six samples examined. No mature oocytes were encountered, leading to the assumption that this species may be hermaphroditic (probably with a seasonal reproductive cycle). The phylogenetic relationship of *Chondrocladia* to the other genera of the Cladorhizidae is discussed, based on the presence of an aquiferous system with choanocyte chambers as the basic 'bauplan' of sponges, which is lost in the other genera. ❐ *Porifera, Cladorhizidae, deep-sea, food-poor environment, adaption, aquiferous system, choanocyte chambers, macrophagy, carnivory.*

Bettina Kübler, (e-mail: bkuebler@ifm.uni-kiel.de), Körnerstraße 3, 24103 Kiel, Germany; Dagmar Barthel, Chemin du Bonnier 9, 1380 Lasne, Belgium; *received 5 October 1998.*

Carnivory is an extremely rare feeding strategy among Recent sponges, with confirmed records so far only from the Cladorhizidae, which is a typical deep-sea family restricted to the bathyal, abyssal or even hadal zones. However, Vacelet (1999, this volume) suggests that several other poecilosclerid families are also likely to contain carnivorous species, as judged by their published descriptions. Carnivory was first discovered in *Asbestopluma hypogea* (Vacelet & Boury-Esnault, 1995, 1996), from a Mediterranean shallow-water cave where the habitat resembles that of the deep-sea (Vacelet et al., 1994). In adaption to its food-poor environment *A. hypogea* developed a carnivorous feeding strategy. The organism is no more than 15mm high, carrying long, thin filaments on its slim main axis, on which swimming prey is captured and overgrown by sponge cells within hours. Vacelet et al. (1995) also described carnivory in a *Cladorhiza* sp., a sponge from a mud volcano in the Barbados Trench that has developed a symbiosis with methanotrophic bacteria: 'The sponge morphology, erect with branching processes bearing a cover of hook-like spicules, suggests that they may also feed on swimming prey ... This was supported by the presence of debris from small crustaceans on the sponges. So far, nothing is known about the feeding strategy of the third genus of the Cladorhizidae, *Chondrocladia*.

The deep-sea sponge *C. gigantea* (Lundbeck, 1905) has a remarkable morphology that has always fascinated scientists. The giant clubsponge, whose skeleton is built by styli and collagen, carries spheres filled with water on little stalks. These are situated mostly on the upper part of its main body, which is slim and erect, rooted in the muddy substratum. The tallest known specimen is 600mm long and has a maximum width of 50mm. From in situ photographs thin-walled spheres are seen to be translucent, whereas when brought to the water surface 'the spheres at the tip of the branches are shrunk into the somewhat oblong, clavate, relatively massive structures characteristic of the branches of a number of *Chondrocladia* species ...'(Tendal et al., 1993) (Fig. 1). Like the main body and stalk these spheres have a certain firmness attributed to the presence of collagen and styli, but are additionally covered by hook-like isochelae.

FIG. 1. In situ photograph of *Chondrocladia* sp., by H. Sahling at 4,900m depth, 54°18'N, 157°11'W. Estimated extended sponge diameter is approx. 50mm (reproduced with permission from Tendal & Sahling).

FIG. 2. Five different individuals of *C. gigantea* examined in the present study, prior to TEM-fixation. The compact 'bulbs' on the main axis are deflated spheres. The largest specimen measures 20cm in length.

MATERIALS AND METHODS

Five specimens of *Chondrocladia gigantea* were dredged from 480m depth at BIOICE station 2792 in the North Atlantic (67°15.17'N; 18°52.01'W) on 15 August 1995 (Fig. 2). Their lengths varied from 78-98mm and widths of their main axes between 3-22mm. On board samples were preserved for electron microscopy with a double fixation in 1% glutaraldehyde and 1% osmium tetroxyde according to the procedure developed by Langenbruch (1983). Afterwards, samples were desilicified with 5% hydrofluoric acid in sea water. The samples were then stored in 100% ethanol at 5°C.

After two years the samples were embedded in acrylic resin (Unicryl, British Biocell International, Cardiff, UK), and cut into semi-thin (1µm) and ultrathin (60-150nm) sections. The semi-thin sections were examined with a Leitz DM RB light microscope (phase contrast) after staining with toluidine blue, eosin and haematoxylin (all stains provided by British Biocell).

For transmission electron microscopy, the ultra-thin sections, cut with freshly made glass knifes on a Reichert OM U3 ultramicrotome, were placed on slot-grids and the contrast was enhanced by uranyl acetate and lead citrate (adapted from the method of Reynolds, 1963). The photographs were taken on a Zeiss EM9 S2 electron microscope using photo plates. The samples were also used for scanning electron microscopy on a Zeiss DSM 940 microscope with a Nikon camera system.

A formalin-fixed sample of *C. gigantea* collected by Ole S. Tendal at BIOICE station 2085, 754m depth, 4 July 1992 was embedded in paraffin (AgarScientific Ltd, Stansted, UK), sectioned on a Leitz microtome (3-7µm) and stained with toluidine blue.

RESULTS

The main axis of all specimens had an extended aquiferous system with wide canals (200-300µm diameter) (Fig. 3) and oval-shaped choanocyte chambers measuring up to 100µm diameter length (Fig. 4). The canals of the aquiferous system appeared to run through the whole length of the main axis of the stalk, while the choanocyte chambers were found in rows along them. The surface of the main axis seemed to carry pores

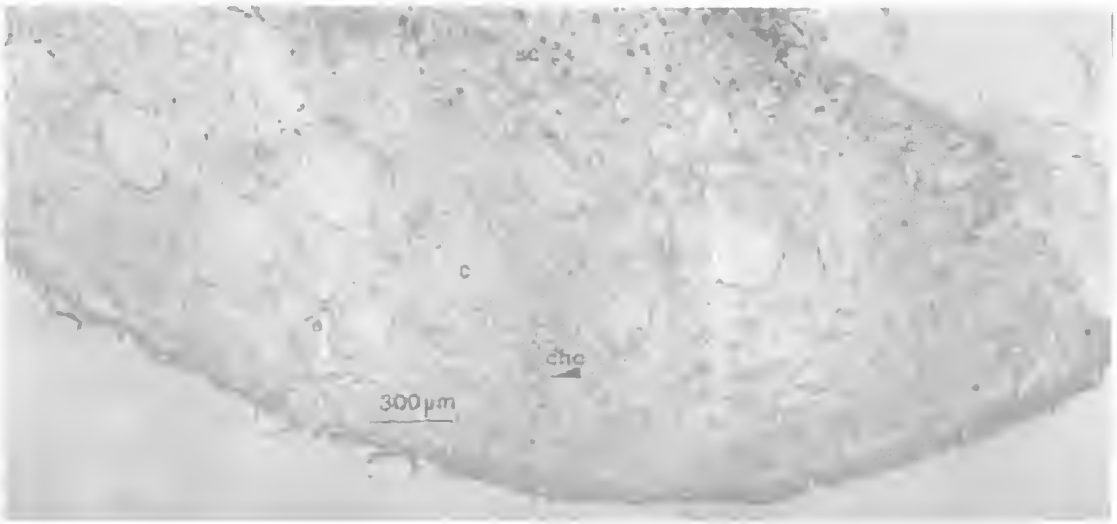

FIG. 3. A cross section through the main axis of *C. gigantea*. The widths of canals measure between 200-300µm. Spermatocysts (sc) gather in the centre of the axis, whereas choanocyte chambers (chc) are situated mostly between canals (c) and surface of the sponge. Phase contrast microscopy.

that were about 160µm wide, narrowing to 20µm diameter. Through these pores diatoms could pass, some of which were found on the walls of the canals. These inlets covered the outside in a regular order, approximately 500µm apart. No choanocytes or ostia were found in the spheres, but canals ran through them and at the distal end of one sphere we noted a few openings (approximately 13) likely to be oscules. However, these structures could as well be caused by deflation.

The main axis and stalks contained only styli, whereas spheres carried styli as well as isochelae and, occasionally, sigmata. The outsides of the spheres were covered entirely with hook-shaped spicules, the microsclerid isochelae, standing closely together like a palisade (Fig. 8). The palisade was then underlain by styli which formed lateral layers or upward protrusions. The thickness of the palisade measured about 70µm. Because of its inflexibility the palisade was partially folded up into the deflated sphere.

Many spermatocysts at different stages of maturity were found in the main axis (Figs 3, 5, 6) and spheres (Fig. 7), all enclosed in cysts. In the middle of the main axis the gametocytes were globular (Figs 5-6) but appeared to elongate when migrating towards the spheres losing their protoplasm (Fig. 7). In one case, a distinct area was visible where cells appeared to form cysts (up to 80µm diameter) and develop into spermatogonia (Fig. 5). More mature stages of

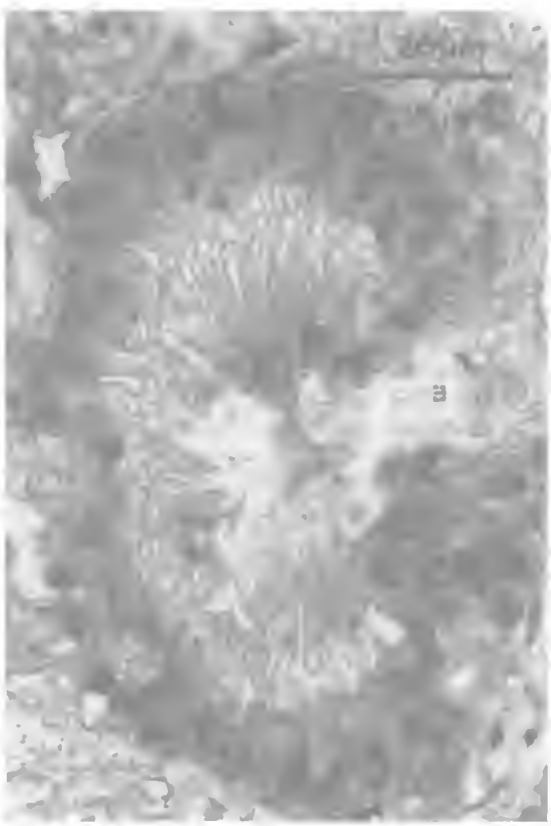

FIG. 4. Oval-shaped choanocyte chamber with apopyle (a) from the main axis. Phase contrast microscopy.

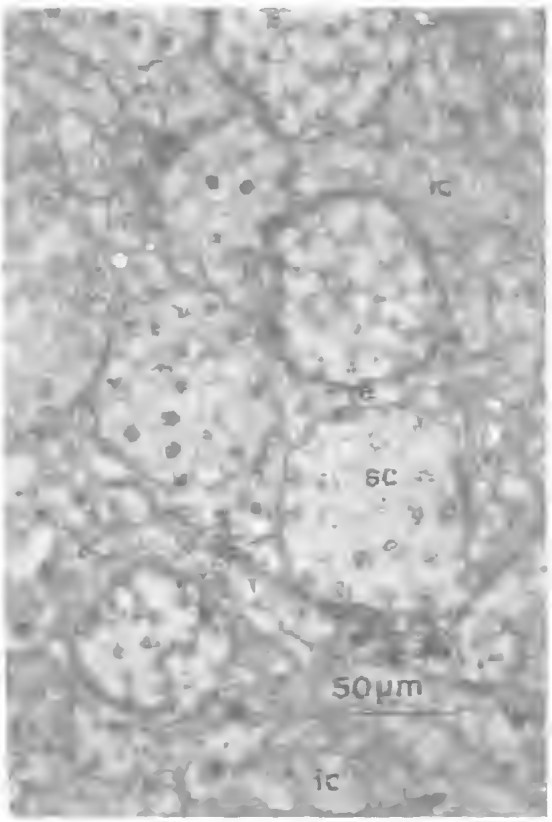

FIG. 5. Spermatocysts from a spermatogonia region in the main axis. Within the cysts (c) the cells (sc) develop simultaneously, but the individual cysts are at different stages of maturity. They are enveloped in epithelial cells (e). Around the cysts are many cells with inclusions (ic) whose function is still unknown. Phase contrast microscopy.

spermatocytes were found on the periphery of this area, the cysts there measuring only 60µm diameter. Even in the spheres the mature spermatozoa remained in cysts. Using semi-thin sections of mature cysts, we estimated that a single cyst contained at least 500 spermatozoa.

Crustaceans in various stages of digestion were abundant only in the spheres, with up to 19 individuals per sphere (Fig. 9). No other prey organisms were noted. Due to their small size or advanced state of digestion, only two species, *Calanus finmarchicus* and *Calanus hyperboreus*, could be determined exactly and were found in greatest abundance (Fig. 10). In one sphere 16 specimens were found probably belonging to *C. finmarchicus*, up to 5.8mm long, and most in the copepodit stage V (Fig. 9).The largest item of prey measured 6.5mm long.

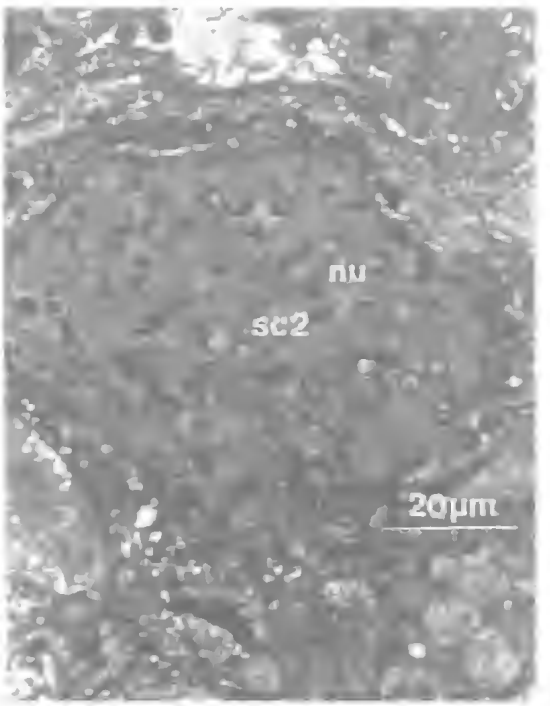

FIG. 6. Spermatocyst in the main axis with spermatocytes that could be in their reduction phase (sc2). The nucleoli (nu) are visible. Condensed heterochromatin can be seen as dark rings on the nuclei. Phase contrast microscopy.

Muscle tissue was found both inside the chitin cuticule of crustaceans surrounded by archaeocytes (Fig. 11) that had migrated towards the prey, and as inclusions in cells (Fig. 12a). Whereas in the first case the tissue still appeared to be intact, showing its striation, pieces of muscle tissue within inclusion cells showed different stages of digestion. In the ones most digested striation was no longer visible, and the inclusions consisted of a more-or-less homogenous mass.

In the outer layer of the main body globular structures of up to 5mm diameter were found being distinctly different from the surrounding sponge tissue. Consisting only of inclusions, they were enveloped in a layer of collagen with an average thickness of 30µm.

Bacteria were found extracellularly in the sponge tissue as well as in massive gatherings of different sizes, especially inside the chitin cuticule of half-way digested crustaceans where they were no longer intact.

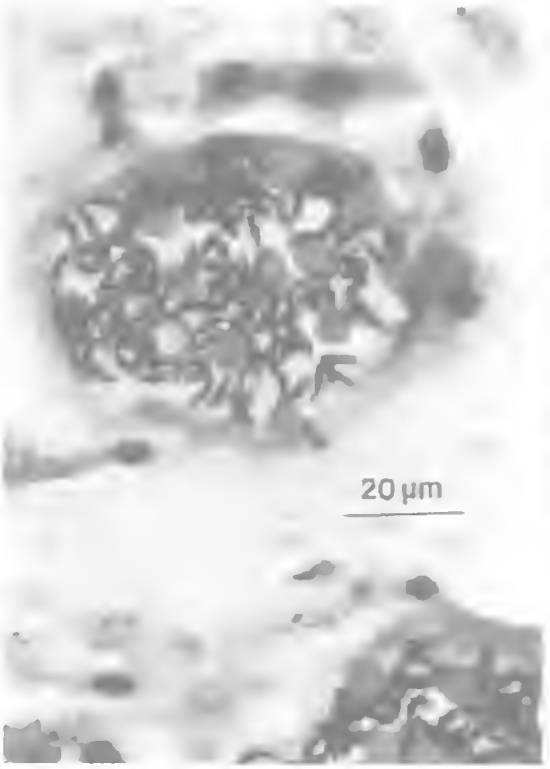

FIG. 7. Cyst with elongated, more mature spermatocytes inside a sphere. Phase contrast microscopy.

DISCUSSION

Our investigations showed that *C. gigantea* has developed carnivory like other members of the family, but with a major difference: whereas the other genera have apparently lost their aquiferous system, *Chondrocladia* still possesses it.

AQUIFEROUS SYSTEM. Water is drawn into the main body through pores and then 'pumped' through canals into the spheres. The water current probably flows unidirectionally, from the base of the organism to the top, since the spheres are predominantly in the upper part of the sponge. It is probably not only collagen and spicules that keep this slim organism upright, but also the water pressure within the sponge. The spheres must be filled with water via the stalks. This is the reason why they appear translucent in in situ photographs and possess little biomass in relation to surface area. Water is assumed to be expelled through oscules on the spheres.

FUNCTION OF THE AQUIFEROUS SYSTEM AND THE SPHERES. The presence of wide canals running through the main axis and rows of

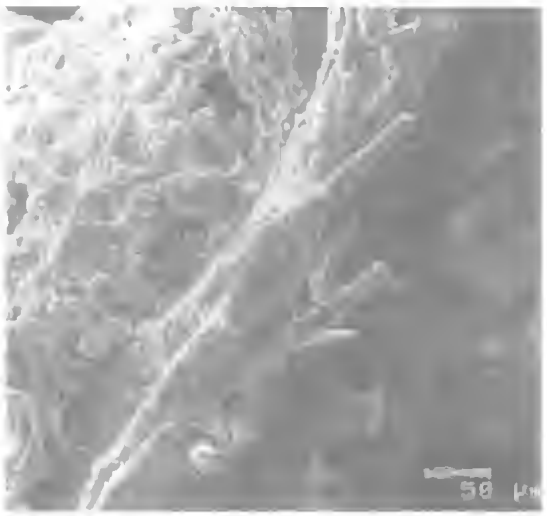

FIG. 8. A palisade of isochelae (isp) on the surface of a sphere. Underneath a criss-cross layer of megascleres (ms), which are simple styli. Scanning electron microscopy (SEM).

choanocyte chambers allow this tall, but slim, sponge to perform an exceptional feeding mode. The spheres can be explained as structures used to catch prey. When observed in situ (Fig. 1) they are usually filled with water and are seen as extended, thin-walled, translucent spheres. It is likely that passing crustaceans are caught on the protruding palisade of microscleres with their many thin appendages. As suggested by Tendal & Sahling (1997), a sphere can probably collapse within tens of seconds. Through the mechanical stimulus of the prey the sphere ejects its water contents through openings at its distal end. Collapsing very quickly, the crustacean is hooked and completely surrounded by sponge tissue so it cannot escape. The crustacean is then digested. Apparently archaeocytes migrate towards the prey and ingest pieces of muscle tissue (estimated size 200µm³). These archaeocytes are then inclusion cells and migrate through the sponge tissue of the spheres into the main axis. The muscle tissue was often found in rectangular shapes leaving the impression that it was dissected into distinct pieces. Aggregations of pieces of muscle tissue that were observed close to the areas where spermatogonia were formed suggest that their protein content may be utilised for the build-up of reproductive cells.

REPRODUCTIVE CELLS. Only male gametogonia could be clearly recognised, although the presence of very young oocytes in the same

FIG. 9. Contents of a sphere from a formalin-fixed sample. The largest crustacean is a *Calanus* species, copepodit stage V, measuring 5.8mm.

specimen where spermatocytes were noted cannot be precluded (Kübler, 1998). The presence of spermatocytes in at least two out of six individuals and the lack of mature oocytes may indicate successive hermaphroditism. Spermatocytes were obviously produced very quickly, while oocytes seemed to take more time. Our investigations support the hypothesis that sexual reproduction plays an important role even in deep-sea organisms, as stated by Witte (1996) for other deep-sea demosponges. Finding mature stages of male reproductive cells and very young oocytes confirms the idea that seasonal reproduction also takes place in greater depths due to dependence on food availability, i.e. productivity of the surface waters, in this case in the form of crustaceans. The hypothesis that asexual reproduction in the form of budding could take place in this species (Tendal & Barthel, 1993) nevertheless cannot be precluded.

Since the most mature stages of spermatocytes were found in cysts within the spheres, complete cysts may be released into the surrounding water, possibly ejected through the distal openings on the spheres concurrent with the expulsion of water. This would be a mode of reproduction similar to that described by Vacelet & Boury-Esnault (1996) for the related species *Asbestopluma hypogea*.

According to Tuzet (1930), Fincher (1940) and others, archaeocytes constitute the source of spermatogonia in Porifera. Subsequently it was proposed that choanocyte chambers could be their predecessors (e.g. Tuzet et al., 1970; Paulus, 1989; Barthel & Detmer, 1990). Although in our

FIG. 10. *Calanus hyperboreus* Kröyer, 1838, copepodit stage V, length: 6.5mm.

samples there were choanocyte chambers that apparently disintegrated to almost the same size as spermatocysts, spermatogonia could also be formed from archeocytes that contain inclusions. Theoretical considerations to calculate cell numbers in choanocyte chambers and spermatocysts (spermatocytes 2 and spermatids) led to the result that choanocyte chambers (with about 1,500 cells) possess roughly two to three times more cells than mature spermatocysts, with the consequence that they probably would not originate directly from choanocyte chambers. In addition, young spermatocysts gathered in certain areas towards the centre of the main axis, whereas choanocyte chambers were regularly distributed and orientated towards the surface of the main axis (Fig. 3). Thus, choanocytes would have to migrate towards the centre to form cysts. In addition to spermatogenesis another reason for disintegration of choanocyte chambers may have been poor preservation of parts of the sponge tissue.

CRUSTACEANS. Most of the crustaceans found in the spheres belonged to two species that are very common in this area of the Norwegian Sea. Almost all of these were in the last copepodite stage (V), which usually sink to the bottom of the sea in late summer to hibernate (e.g. Orr, 1934; Raymont, 1963). It can be assumed that the sponge neither selects its food nor has any food preferences.

GATHERINGS OF INCLUSIONS. The function of gatherings of inclusions to build globular structures up to 5mm diameter in the main body could not be clarified. Originally, they were interpreted as embryos by Lundbeck (1905), but this could not be subsequently proven since no embryonic structures were found. Possible alternative interpretations are that these are places where by-products are deposited, or they may be

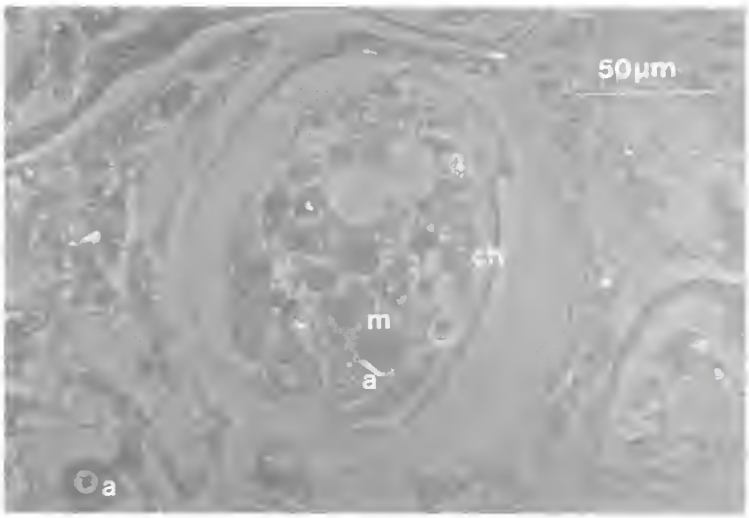

FIG. 11. Pieces of intact muscles (striated) within an extremity of a crustacean found in a sphere (m, muscle; a, archaeocytes; ch, chitin cuticule). Phase contrast microscopy.

depots of nutrients. The latter interpretation makes most sense given the food-poor environment in which *C. gigantea* lives, and the presumably vicarious seasonal food availability, but there is so far no empirical support for either hypothesis.

BACTERIA. The role of bacteria in this species was not clarified from our investigations. The fact that masses of bacteria, which did not look intact, were found close to or within prey in the sponge tissue, provides two possible assumptions: 1) either bacteria are digested by the sponge, which would mean, that this species is optionally bacterivor, or 2) bacteria facilitate digestion of prey organisms.

We assume that in *C. gigantea* the presence of an extended aquiferous system, which in other sponges is used to filter food particles (e.g. Simpson, 1984), is modified to an elaborate mechanism to catch prey. The spheres, which are part of this mechanism, also distribute the sponges' sexual products into the surrounding water.

Whereas closely related species like *A. hypogea* catch their prey (also consisting of crustaceans) by overgrowing it, *C. gigantea* catches its prey by inflating its spheres (probably within tens of seconds; Tendal & Sahling, 1997). Both species react to the mechanical stimulus induced by crustaceans landing on the external surface.

Living as a predator (macrophagy) instead of a filter feeder (microphagy) is a typical adaption to the deep-sea environment (Gage & Tyler, 1991). However, as noted above, feeding on bacteria and/or food particles in the water column, subject to their seasonal availability, cannot be excluded. Thus, the sponge would have maintained its original feeding strategy as a filter feeder and added carnivory as a new, supplementary method.

The peculiar morphology of this sponge may reflect its adaptation to the extreme, food-poor, deep-sea habitat in which it lives by reducing its main axis to a thin stalk that reaches into currents above the bottom and forming surface extensions through thin-walled spheres, thus providing a maximum chance to catch prey utilising minimal sponge material, i.e. body mass, as possible.

Our interpretation of the presence of choanocyte chambers and canals in *C. gigantea*, which are not present in other carnivorous sponges such as *A. hypogea* or *Cladorhiza* sp., is that *Chondrocladia* possesses the basic sponge 'bauplan' and thus stands at the base of the Cladorhizidae. The affiliation of Cladorhizidae within Porifera has been questioned due to its lack of the 'typical' sponge feature (viz. filter feeding using an aquiferous system with choanocyte chambers creating a water current; Vacelet & Boury-Esnault, 1995). Our data show that this feature is certainly present in *C. gigantea*, and consequently the family certainly belongs to Porifera. *Chondrocladia* is a binding link between the original microvorous and the specialised carnivorous species which have lost important anatomical characteristics. In contrast to related cladorhizid species the conversion from particle-feeding to carnivory in *C. gigantea* is not fundamentally linked to the loss of the aquiferous system, but is a functional modification (and maybe optional use) of existing structures.

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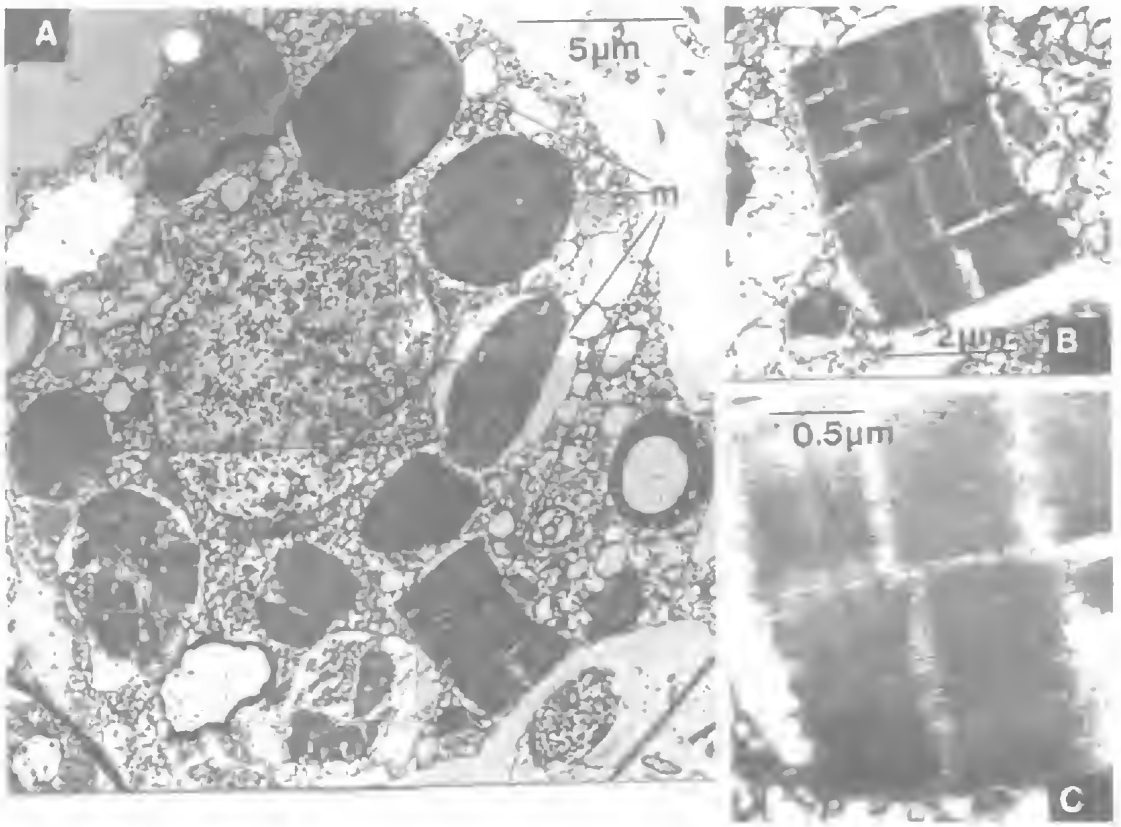

FIG. 12. A, inclusion cell from the main axis containing at least twelve pieces of muscle tissue (m). From the bottom right to the top left a succession of increasingly digested pieces can be observed. While the least digested ones still possess their striation, the more digested ones are homogenous inclusions. In the middle of the cell there is a nucleus. Transmission electron microscopy (TEM). B, enlarged view of a piece of muscle least digested in this cell. TEM. C, enlarged view of the striation of the muscle fibre. TEM.

to discussions, and to Heiko Sahling (GEOMAR, Kiel) for providing the in situ photograph of *Chondrocladia* sp. We are also grateful to H. Flügel for technical advice on the TEM and R. Schmaljohann (both Institut für Meereskunde Kiel) on the SEM. Thanks also to J. Hoeg for introducing us to his methods for preparing material for electron microscopy and P.V. Jensen (both Department of Cell Biology, University of Copenhagen) for assistance in histological questions. The manuscript benefitted from the comments of two anonymous reviewers.

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REMARKS ON THE PALEOECOLOGY AND REEF BUILDING POTENTIAL OF LATE JURASSIC SILICEOUS SPONGES. *Memoirs of the Queensland Museum 44: 297 1999:-* In the early Late Jurassic (Oxfordian) siliceous sponges developed extensively. They formed a discontinous siliceous sponge reef belt extending over more than 7000km from New Foundland, Iberia, France, Switzerland, Germany, Poland, Romania to the Caucasian Mountains.

Siliceous sponges are no systematic unit but belong to the different taxonomic groups Hexactinellida and the polyphyletic lithistid demosponges. Due to their different organisation and biology, the ecological demands of the different siliceous sponges groups differ remarkably. The two major groups must be carefully distinguished for palaeoenvironmental interpretations.

In general, lithistid demosponges are active filter feeding organisms. They feed on nannoplancton mainly bacteria. The bathymetric distribution of demosponges corresponds to a great extent with the bathymetric distribution of bacteria. The fairly high preservation potential of rigid demosponges is explained by a high amount of mesohyl-dwelling bacteria, causing rapid calcification after death.

Osmotrophy is an important feeding strategy of Hexactinellida. Dissolved organic matter is enriched in deeper water low-energy settings, causing the majority of Hexactinellida to dwell in such habitats. As the mesohyl of Hexactinellida consists of very thin collagenous material, there is hardly any room to harbour bacteria. This easily explains why microbially induced post-mortem calcification of the sponge by microbial automicrites occurs at a much lower rate so that fossilisation potential is much lower in comparison with rigid demosponges.

The taxonomic composition of fossil siliceous sponge populations is mainly controlled by sedimentation rate, nutrition and hydrodynamics. The dominance of major taxa is strongly influenced by bathymetry, due to changes of hydrodynamics and nutrition along a bathymetrical gradient. However, the quality of substrates, water energy or extreme oligotrophy may strongly modulate bathymetric distribution. ❐ *Porifera, Late Jurassic, Hexactinellida, lithistid Demospongiae, palaeoecology, calcification, fossilisation.*

Manfred Krautter (email manfred.krautter@geologie.uni-stuttgart.de), Institut für Geologie und Paläontologie der Universität,, Herdweg 51, D-70174 Stuttgart, Germany: 1 June 1998.